THE ALLEGED SYNONYMY OF *LYCORHINUS* AND *HETERODONTOSAURUS*

By

A. J. Charig

British Museum (Natural History), London

&

A. W. Crompton

Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

(With 11 figures.)

For more than half a century the only pre-Jurassic ornithischian known was *Geranosaurus atavus* Broom, 1911, an incomplete lower jaw (with some doubtfully associated postcranial bones) from the Upper Triassic Cave Sandstone of South Africa. In 1962, however, Crompton & Charig gave a preliminary description of an almost complete and extremely well-preserved skull, also from the Cave Sandstone, which they named *Heterodontosaurus tucki*. One of the most remarkable features of *Heterodontosaurus* is its dentition, shown in Figures 10 and 11. There are (*a*) simple pointed premaxillary teeth working against a toothless predentary, (*b*) one enlarged pointed caniniform tooth in each jaw, this being the last premaxillary tooth in the upper jaw and the first dentary tooth in the lower, and (*c*) more complex, closely packed maxillary and dentary teeth, with ridged lateral and medial surfaces and with enamel on one side only, abrading and sharpening each other like opposing chisels to produce oblique, flat, continuous occlusal surfaces. These cheek teeth are set in from the side of the face. Most curious of all, there seems to be no tooth replacement whatever in the type skull of *H. tucki* or in another nearly complete skull of the same species collected subsequently (S.A.M. No. K1332). In their original description Crompton & Charig noted also the verbal observation of their colleague, J. Attridge, that an incomplete dentary from the underlying Red Beds (Figs 8, 9), described by Haughton in 1924 as *Lycorhinus angustidens* gen. et sp. nov. and believed to belong to a cynodont, possessed a dentition very like that of *Heterodontosaurus* and probably represented an ornithischian dinosaur rather than a therapsid. Romer (1966) classified *Lycorhinus* as an ornithischian, placing it tentatively in the family Hypsilophodontidae of the suborder Ornithopoda. A very detailed description of the holotype skull of *Heterodontosaurus tucki* has now been prepared by Charig & Crompton (in press) and it is intended that a similar description of S.A.M. No. K1332 shall follow.

Since 1962 Upper Triassic ornithischians have been turning up more often, mostly in the Stormberg Series of southern Africa (Republic of South Africa and Lesotho) but elsewhere too. Until now, however, only one other Stormberg ornithischian has been named—*Fabrosaurus australis* Ginsburg, 1964—and once again the holotype consists of nothing more than a fragment of a dentary from

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the Red Beds. This has virtually no distinguishing features other than the highly characteristic features of its teeth, which are clearly very different from those of *Heterodontosaurus*. In *Fabrosaurus*—if we assume its complete dentition to have been like that of similar specimens discovered later (Fig. 1)—the heterodonty is less marked, without development of caniniforms; the more posterior teeth are of a leaf-like shape, probably not very different from the unworn teeth of *Heterodontosaurus* but more widely spaced and never worn down to a flat continuous occlusal surface; the cheek teeth are not set in from the side of the face, and normal alternating reptilian replacement appears to occur. We think it very likely that such teeth will prove to be common to several early ornithischian genera as well as to persistently primitive forms of later date, e.g. *Echinodon* Owen, 1861 from the Purbeck Beds of England (on the Jurassic–Cretaceous boundary). Indeed, this 'fabrosaur' type of tooth is accepted by all workers as primitive for the Ornithischia; Bakker & Galton (1974) are even claiming that the basic pattern of the dentition in primitive ornithischians (such as *Fabrosaurus*) was similar to that of small prosauropods. But if this characteristic tooth structure is diagnostic of a whole family (or of an even higher taxon) rather than of a single genus, then the nominal genus *Fabrosaurus* must be indeterminate. The names *Fabrosaurus* and *F. australis* must therefore be regarded as *nomina dubia*; no other material should be referred to the species, and no other species to the genus.

Thulborn has nevertheless described more ornithischian material from the Stormberg Series, including both skull (1970*b*, 1971*a*) and postcranial elements (1972), and he refers it all to *Fabrosaurus australis*; he does so because of the 'highly distinctive' nature of the teeth (Fig. 1). But for the reasons given above, and because it is evident from our own collections that the Stormbergs of southern Africa contain other, hitherto undescribed ornithischians, we cannot accept that Thulborn's reference of this material to *F. australis* is justified—even though the reptile he described is again very different from *Heterodontosaurus*. We should prefer to call it 'fabrosaurid gen. et sp. indet.'.

It is therefore apparent that all the Triassic ornithischians that have been found in southern Africa up till now (even the little-known *Geranosaurus*) may be classified as either '*Heterodontosaurus*-like' or '*Fabrosaurus*-like', according to the nature of their teeth. The rest of this paper is mainly concerned with those resembling *Heterodontosaurus* in this respect.

Our greatest concern is with Thulborn's contention (1970*a*) that *Lycorhinus angustidens* and *Heterodontosaurus tucki* are congeneric, i.e. that the nominal genus *Heterodontosaurus* Crompton & Charig, 1962 is a subjective junior synonym of *Lycorhinus* Haughton, 1924, is therefore invalid and should be discarded. (At the same time he agrees that the skull from the Cave Sandstone merits specific separation as *L. tucki*.) In consequence he now uses the name *Lycorhinus* instead of *Heterodontosaurus* in his published discussions on ornithischian phylogeny (1970*a*, 1971*a*, *b*, 1972), sometimes adding the name '*Heterodontosaurus*' in parentheses or square brackets with or without inverted commas. He also con-

tends (1970*a*, 1971*b*) that both valid genera of ornithischians from the Upper Trias of southern Africa (i.e. *Lycorhinus* and *Fabrosaurus*, according to him) should be placed in the family Hypsilophodontidae, the type-genus of which is Wealden in age; and (1971*b*) that these Upper Triassic forms should be classified further into two subordinate 'groups' of that family, to be called 'lycorhinids' and 'fabrosaurs' respectively.

In this connection it should be mentioned that in Britain and the U.S.A. there are—apart from Thulborn himself—four established palaeontologists who have worked on primitive ornithischians within the last few years: Charig, Crompton, Galton and Ostrom. None of the four accepts Thulborn's synonymy. Nor does Cluver, Curator of Fossil Vertebrates in the South African Museum, the museum where all the material of both genera is housed. Why, then, should we bother to discuss the synonymy further? We do so partly to determine our position in relation to such a declared synonymy, whether we are free to accept it or reject it as we think fit, and partly to consider, if we *are* free to reject it, whether we should be justified in so doing. But we are less concerned with resolving this particular case than with using it as an illustration of certain general points, especially the inadvisability of publishing a synonymy without logical consideration of all the available evidence and without due regard for its taxonomic and nomenclatural consequences.

What, then, are our opinions of the generic synonymy proposed by Thulborn? First, we believe that such a synonymy can serve no useful purpose whatever; indeed, from a practical point of view it is highly undesirable. We shall explain this further below. Secondly, it seems to us that the synonymy is based upon alleged similarities for which the evidence, in many instances, is either incorrect or not pertinent or both; that, because of the fragmentary nature of the *Lycorhinus* material, the only useful evidence concerns the lower teeth; that there is as much evidence of differences between the teeth of the two genera as of similarities; and that this severe limitation of the comparison, coupled with our lack of knowledge of the variability of the tooth structure of Triassic ornithischians, would probably make it difficult, if not impossible, to estimate the closeness of the relationship between the two holotypes. Did they belong to the same genus, as claimed by Thulborn, or only to the same subfamily? Perhaps only to the same family? Obviously this problem requires detailed consideration.

Before embarking on this, however, we shall deal briefly with Thulborn's other contention, concerning his two special 'groups' within the family Hypsilophodontidae. These, being suprageneric, are manifestly of subfamilial rank and should be recognized as such; yet one of the names he gives to those subfamilies is incorrect in its stem, irrespective of whether or not his synonymy be accepted, and both names are incorrect in their terminations (even in their vernacular forms). Our first objection to Thulborn's subfamily names is based on the provisions of Article 40 in the International Code of Zoological Nomenclature, which states: 'Synonymy of the type-genus. When, after 1960, a

nominal type-genus is rejected as a junior synonym (objective or subjective), a family-group name based on it is not to be changed, but continues to be the valid name of the family-group taxon that contains both the senior and junior synonyms.' In other words, a family or subfamily name must be retained even though the type-genus on which it is based has been rejected as a junior synonym. Applying this to our particular case, the family name Heterodontosauridae Kuhn or Romer (which?), 1966 could not be replaced by a new family name Lycorhinidae, even if *Heterodontosaurus were* accepted as a junior synonym of *Lycorhinus*; and the same is true of the corresponding subfamily names. As for our second objection, Article 29 of the Code lays down that 'A family-group name is formed by the addition, to the stem of the name of the type-genus, of . . . -INAE in the case of a subfamily'. Thulborn's two 'groups', therefore, should be called Heterodontosaurinae and Fabrosaurinae respectively. In any case, Galton (1972) has already pointed out the undesirability of placing these Triassic forms within the Hypsilophodontidae; although we do not agree with every aspect of Galton's phylogeny and classification, we do agree with him that Thulborn's two 'groups' merit independent familial status, as Heterodontosauridae and Fabrosauridae. (Authorship of the latter family is attributable to Galton 1972.)

Let us return to our central theme—the matter of the alleged generic synonymy. It sometimes happens that the Law of Priority (Article 23 of the Code) obliges one to place a well-established, familiar name in the junior synonymy of one much less familiar or altogether unknown; or, even more unfortunate, to place a taxon based on excellent type-material in the subjective junior synonymy of another based on poor type-material. The placing of *Heterodontosaurus* in the junior synonymy of *Lycorhinus* would have both these unhappy consequences without any possible advantage accruing therefrom. *Heterodontosaurus* is already a well-established name appearing in many articles and recent textbooks, for, as the first fairly complete skull of a Triassic (or indeed pre-Upper Jurassic) ornithischian, it attracted a great deal of attention; *Lycorhinus* is a name familiar to no one and, where it does appear in lists of genera (e.g. in Romer 1956), it has usually been classified as a therapsid. The *Heterodontosaurus* holotype has now been completely developed and the detailed description of its skull (Charig & Crompton, in press) is likely to make it the most completely described dinosaur skull in existence; moreover (as mentioned above) there is now another skull (S.A.M. No. K1332), equally good if not better, in association with good postcranial material. The *Lycorhinus* holotype, on the other hand, was an incomplete left dentary, with eight teeth and the impressions of four others, and is today (see p. 174) represented only by the most anterior, caniniform tooth, and the impression of the dentary with its row of posterior teeth (S.A.M. No. 3606). If the two holotype specimens *were* congeneric, beyond all reasonable doubt, and if we were given the choice of which to use as our standard of reference for the combined genus, the choice would obviously fall upon *Heterodontosaurus*; the use of the now very fragmentary

Lycorhinus type would impose great practical difficulties.

But we should have no such choice. *L. angustidens* is the type-species of *Lycorhinus*, and must remain so. The true systematist is like a judge in a civil case; he must apply the law impartially, interpreting it rigidly where the wording is unequivocal even though he may think it to be unjust. To disregard the law (even in some small particular) or to permit others to do so can only bring about a general disregard for the law as a whole. If the systematist feels that a certain Rule should not be applied in a certain case, he can request the International Commission on Zoological Nomenclature to exercise its plenary powers; if he thinks that a particular Rule or part thereof is a bad rule, his remedy is to seek to change it through the next Congress. The wisest course, however, for anyone suspecting that a possible synonymy might prove inconvenient or embarrassing could well be to ignore it altogether; on the other hand, once it has been dragged into the open it must be judged on only one aspect—not on its consequences or its practicability but simply on whether or not it is possible to show, to the reasonable satisfaction of other workers in the field, that the specimens or taxa concerned are sufficiently alike to be given the same name. Charig & Reig (1970) state that: 'In deciding synonymy or otherwise the onus of proof lies with him who wishes to establish it.' Kermack, Mussett & Rigney (1973) are even more positive: 'Once a genus has been described and named, the onus is entirely on those who wish to make the name a synonym to show that the two genera concerned are identical *beyond any possible doubt* [their italics]: the onus is in no way on those who wish to maintain the *status quo* to prove that the names are not synonyms.'

This is the case with *Lycorhinus* and *Heterodontosaurus*. It should have been obvious to Thulborn that, even if he could have proved the synonymy, here was a case for letting sleeping dogs lie; but once he had chosen to stir them up we found ourselves compelled to examine his arguments very carefully in order to determine the degree of acceptability of his conclusions. We have done this as objectively as possible, well aware of the fact that, as co-authors of the name *Heterodontosaurus*, we might be accused of some emotional attachment thereto!

Essentially Thulborn's arguments for synonymizing *Heterodontosaurus* with *Lycorhinus* rely upon a new specimen, U.C.L. No. A.100 (Figs 4–7); he claims that this specimen, a block of sandstone with dissociated pieces of skull, is a topotype of *L. angustidens*. (While he admits that the holotype of *L. angustidens* did not provide enough evidence even to investigate the possibility that *Lycorhinus* was an ornithischian, apparently a latex impression of that holotype now affords sufficient proof of its specific identity with A.100!) A.100, in turn, is regarded as congeneric with *Heterodontosaurus tucki*.

The first question is, is such use of intermediate specimens legitimate? If the holotype of one species cannot be synonymized generically with the holotype of another, is it proper to synonymize one with an assumed topotype—or even a mere referred specimen—of the other? The answer to this question,

in general, is indubitably yes. It may well be that two well-preserved but incomplete holotypes in the same deposit consist of different parts of conspecific individuals but cannot be shown to belong to the same species until a new, more complete specimen including both parts associated proves to be identical to both. For example, most species of chelonian in the London Clay are based either on skulls or on shells; it is likely that many 'skull species' could be paired up with 'shell species', but this can be done only by the finding of well-preserved specimens with skull and shell in association. Such specimens are rare.

The case of *Lycorhinus* and *Heterodontosaurus*, however, is not like that at all. All that we have of *Lycorhinus angustidens* is an impression of the dentary, an element of which the greater part is present also in the holotype of *Heterodontosaurus tucki*; the use of another dentary as an intermediate cannot help matters at all because, without any additional elements in common to the two specimens concerned, we are no better equipped to prove the identity of *that* dentary with the *Lycorhinus* holotype either. Indeed, even if we were provided with an absolutely perfect skull as our intermediate we should not be able to prove that its dentary and lower teeth were identical with those of *Lycorhinus angustidens*, although we might be able to prove the identity of that perfect skull with the type skull of *Heterodontosaurus tucki*. The simple fact is that the holotype of *Lycorhinus angustidens* seems to be too incomplete and too poorly preserved to allow anything to be certainly identified with it.

Thulborn fails to comment on the fact that specimen No. A.100 has heavily worn maxillary teeth and unworn dentary teeth; it is interesting to speculate as to how he imagines the animal wore down the former while preserving the latter in their newly erupted condition. This apparent anomaly did lead us to suspect, albeit fleetingly, that the lower jaw of A.100 might not have belonged to the same animal as did the upper jaws; we now regard that possibility, however, as no more than extremely remote because the various elements present on the A.100 block (premaxilla, maxillae, jugals, frontal, postorbital, dentary) show no duplication and are all of commensurate size. In any case, the premaxilla, maxillae and upper teeth all give clear indications of heterodontosaurid affinities, and the lower jaw—except for its unworn teeth—does the same. Even so, we remain puzzled by the unworn condition of those lower teeth. Thulborn, on the other hand, appears to ignore the fact that those unworn lower teeth do not bear much resemblance to any *Heterodontosaurus* teeth described by Crompton & Charig in the holotype of *H. tucki* but are in some respects more reminiscent of the teeth of *Fabrosaurus australis*. The details which he gives of the 'second specimen of *Heterodontosaurus*', which he refers to as being in the care of one of us (A.J.C.) in the British Museum (Natural History), are inaccurate; and, while it seems very likely that the fragment of maxilla in question belonged to a member of the family Heterodontosauridae, it differs in several particulars from the holotype of *Heterodontosaurus tucki*. (Had we known that he intended to mention our research material in his article we should gladly have supplied him with the necessary information.)

Thulborn takes sufficient cognisance of the differences between the lower caniniform teeth of *Lycorhinus* and those of *Heterodontosaurus*—the former crenellated on the anterior[1] margin only, the latter on both margins—to admit that this signifies a specific difference between the two forms. We agree that this difference exists; for we maintain that the type of *Lycorhinus angustidens*, while too incomplete and too poorly preserved to permit anything to be certainly identified with it, was well enough preserved to show that it was different from both A.100 and *Heterodontosaurus tucki*.

Despite this minor difference there is no doubt that all three specimens concerned possess four common characters of the dentition which are typical of the '*Heterodontosaurus*-like' forms and which are lacking altogether in *Fabrosaurus* and its allies, the only other ornithischians from the Upper Trias of southern Africa of which we have any real knowledge. These are (*a*) the prominent caniniform tooth at the front of the dentary, (*b*) a trend towards the possession of closely packed postcaniniform teeth which are worn down to a continuous occlusal surface, (*c*) the apparent complete absence of any tooth replacement (see Charig & Crompton, in press), and (*d*) the mediad recession of the tooth row into the side of the face, suggesting the presence of muscular cheeks (see Galton 1973). Thulborn, oddly enough, draws attention only to the first of these. Characters (*a*) and (*c*) are unique to this particular group within the Ornithischia, but (*b*) is found also in some Cretaceous members of the order and (*d*) in all post-Triassic members.

Let us now analyse Thulborn's comparison of *Lycorhinus* with *Heterodontosaurus*, detail by detail. It relies entirely on the unquestioned acceptance of two points: his unproven, tacit but very evident assumption that all the material on the A.100 block represents a single individual, and his allegedly proven belief that 'specimen A.100 does represent *Lycorhinus angustidens*' (p. 242). We shall—with some hesitation—accept the former point, supposing that all the elements visible on the A.100 block (Fig. 1) belonged to the same animal and ignoring the surprising and seemingly inexplicable fact that the maxillary teeth are heavily worn while the dentary teeth are scarcely worn at all. But we feel that his reference of A.100 to *Lycorhinus angustidens* should be submitted to a critical examination.

The lower jaw of A.100 is exposed only on its lateral side (Fig. 4). Thulborn (p. 241) refers it to *L. angustidens* because, according to him, it shares the following common features with Haughton's holotype:

1. The mandible is exceptionally deep.
2. There is a large, caniniform first dentary tooth, with only its anterior edge crenellated.

[1] Thulborn uses terms employed in dentistry and human odontology when describing the teeth of reptiles; thus anterior becomes 'mesial', posterior 'distal' and so on. We disagree with Edmund (1969) that the use of these terms is convenient and that 'The terms distal and mesial are to be preferred to anterior and posterior because of the curved shape of the dental arcade.' 'Distal', in particular, is generally used by comparative anatomists to mean something entirely different (namely, opposite to proximal) and it is therefore ambiguous or misleading to apply it to reptile teeth.

3. There is a small gap between the first (caniniform) and second dentary teeth.

Haughton, however, described and figured (1924: 343–344, fig. 8; our Fig. 8) only the *medial* aspect of his holotype. Later the specimen itself became separated from the piece of matrix to which it had been attached by its lateral surface and was lost; the *lateral* aspect of the dentary, as evidenced by its natural mould on the matrix, was described and figured by Broom (1932: 307, fig. 104, I; our Fig. 9). It is of this lateral aspect that Thulborn possesses a latex impression (p. 236) and we ourselves have another. But Thulborn does not mention Broom's account of *Lycorhinus* (although it is evident from personal communication that he is aware of its existence, indeed we must acknowledge our gratitude to him for reminding us of it) and he tacitly implies that his latex impression is of the surface described by Haughton, without indicating at this point whether Haughton described the medial or the lateral surface. Later, however (p. 242), Thulborn states that further comparisons are difficult because only the medial side of the *Lycorhinus angustidens* holotype was exposed and described by Haughton, whereas, of course, the mandible and lower teeth of specimen A.100 are visible only in lateral aspect; had Thulborn used his latex impression of the lateral side of the holotype the comparison would have been easier and more meaningful.

Whichever surface of the *Lycorhinus* mandible be compared with the lateral surface of the A.100 mandible, it is immediately obvious to us that the two specimens are different in many respects. With regard to the three similarities cited by Thulborn (see above), the second—concerning the presence of a caniniform with only its anterior edge crenellated—is certainly correct. But the illustrations by Haughton, Broom and Thulborn, taken in conjunction with the latex mould, suggest that the base of the caniniform tooth is relatively more slender in A.100 than in *Lycorhinus*. Further, the tip of the *Lycorhinus* caniniform is bevelled off anteromedially, as shown in Haughton's figure and described in his text; the lower caniniform of A.100 is not exposed on its medial side, but Thulborn's illustration of it in lateral view suggests that the tooth is unworn right up to its remarkably acute tip. (Haughton commented that in *Lycorhinus* it was 'bevelled off by rubbing against the canine of the upper jaw', but, with no upper jaw preserved, this was pure speculation; in *Heterodontosaurus* the upper and lower caniniforms, seemingly in their natural relative positions, are nowhere near each other.) The same illustrations by Haughton, Broom and Thulborn suggest also that Thulborn's other two similarities are not especially close: the mandible beneath the caniniform is much shallower in A.100 than in *Lycorhinus*, and the gap between the first (caniniform) and second dentary teeth is much wider.

There are other differences too, outweighing the similarities in number and importance. The postcaniniform teeth of *Lycorhinus* are inclined slightly forwards, they are so close together that the distal ends of their crowns are in contact with each other, and they are heavily worn down to a continuous,

though rather irregular, occlusal surface. On the other hand, the teeth of A.100 show no forward inclination whatever, they do not touch each other (Thulborn's fig. 5, our Fig. 4, suggests that the third and fourth teeth might have touched before the third was broken) and, as illustrated, they show no signs of wear; this last point is confirmed by Thulborn's description (p. 240). In both specimens a cingulum separates the more or less parallel-sided root from the upwardly widening crown, the anterior and posterior edges of the latter diverging towards the occlusal margin; in *Lycorhinus* this cingulum is absent on the lateral surface and present (*fide* Haughton) on the medial surface, but in A.100 (where the medial surface of the lower teeth is unknown) it is well developed on the lateral surface. The teeth of *Lycorhinus* are not each symmetrical in lateral or medial view, for on each tooth from the fifth onwards ('4th molar' of Haughton) there is 'a large anterior cusp occupying two-thirds of the grinding surface, and a much smaller, somewhat lower posterior cusp' (Haughton 1924: 344); the groove on the medial surface, running between the ridges which descend from the cusps to the cingulum, is therefore markedly posterior in position. But in A.100, where we can see only the lateral surface of the tooth row, each crown has the form of a symmetrical arrowhead; there are three or four small cuspules on either side (anterior and posterior) of the tip, and the well-pronounced ridges which run down from each cuspule are roughly symmetrical on either side of a stronger central ridge. (It must be admitted that the lateral surfaces of the teeth of the *Lycorhinus angustidens* holotype, as figured by Broom and as shown in the latex mould, *do* look a little more symmetrical than the medial surfaces, but they are still quite unlike the lateral surfaces of the teeth of A.100.)

Because of the difficulties alleged by Thulborn of comparing the lower teeth of *Lycorhinus* with those of A.100 (difficulties which, as we have seen, are actually unnecessary if use be made of Broom's description and figure and of the latex mould), Thulborn also compares the medial aspect of the dentary teeth of the former—as described and figured by Haughton—with the medial aspect of the *maxillary* teeth of A.100 (Fig. 7); this comparison, of extremely dubious validity, enables him to claim (p. 242) of the teeth in the latter specimen that their 'worn crowns (Fig. 4) are virtually identical with those described and figured by Haughton (1924). In each case the lingual crown surface bears a broad median rib and the distal [posterior] margin is produced as a thin and erect ridge, the mesial [anterior] edge showing only a faint tendency towards elaboration into a similar ridge.' In fact none of these features is apparent in Haughton's figure of the *Lycorhinus* holotype or mentioned in his description, unless we include 'the ridges which descend from the cusps to the cingulum'. According to Thulborn, these alleged but actually non-existent similarities between the upper teeth of one specimen and the lower teeth of another 'leave little doubt that specimen A.100 does represent *Lycorhinus angustidens*'. We repeat that the medial surfaces of the dentary teeth of A.100 remain unknown and may well differ from those of the maxillary teeth; but they could not have

resembled the corresponding surfaces in *Lycorhinus*, for, as indicated above, the dentary teeth of A.100 are unworn and their whole shape is quite different from that found in *Lycorhinus*.

Thulborn goes even further and states (p. 236) that: 'Since both of these specimens are from the same locality there is a slight possibility that they might represent different parts of a single individual, though this seems unlikely in view of the great hiatus between their two dates of collection.' He ignores the several differences that we have pointed out between *Lycorhinus* and A.100, evidently preferring to believe that it is possible for the teeth on the left dentary to undergo extensive wear while those on the right dentary of the same animal remain virtually unworn! He also ignores the fact that the exposure of the Red Beds at Paballong (neither Haughton nor Thulborn localized their specimens more precisely than that) is so large as to render negligible the chances of two bones found on different occasions being parts of the same individual—especially when those two occasions are separated by more than 40 years. In any case, the rate of erosion at Paballong during the rainy season is so high that the time required for the destruction of a piece of bone weathered out of the rock is more likely to be, on average, a matter of days or even hours rather than of decades.

In conclusion, we are much less impressed by Thulborn's similarities between *Lycorhinus angustidens* and A.100 than by the differences between them; and we feel that we have established a *prima facie* case for their generic separation.

Because of his determination of A.100 as *Lycorhinus augustidens* Thulborn next claims that 'Specimen A.100, imperfect though it is, considerably amplifies our knowledge of *Lycorhinus*', and then proceeds, in the light of that 'amplified' knowledge, to compare *Lycorhinus* with the holotype of *Heterodontosaurus tucki*; in that comparison he draws his *Lycorhinus* characters partly from the holotype, partly from the A.100 lower jaw, but mostly from the upper jaw and skull of A.100. He concludes that: 'Whilst there are definite differences between *Lycorhinus angustidens* and *L.* (*Heterodontosaurus*) *tucki* these serve only to distinguish the animals at species level and do not warrant their separation into distinct genera.' But we have rejected his determination of A.100 as *Lycorhinus angustidens*. In that circumstance *Lycorhinus* and A.100 should be compared separately with *Heterodontosaurus*: first the holotype dentary of *Lycorhinus* with the dentary of the holotype of *Heterodontosaurus*, then the dentary of A.100 with the dentary of the holotype of *Heterodontosaurus*, and finally the various elements of the upper jaw and skull of A.100 with the corresponding elements of the *Heterodontosaurus* upper jaw and skull. Further, since we believe that *Lycorhinus* and A.100 are *not* identical, it follows that—in our view—*Heterodontosaurus* cannot be the same as both of them; it may be *either* the same as *Lycorhinus*, *or* the same as A.100. (If it is not the same as A.100, then the latter must represent yet another ornithischian in the Upper Trias of southern Africa.) It is even possible that *Heterodontosaurus* is not the same as either *Lycorhinus or* A.100, in

which case we must be dealing with *three* separate forms.

First let us compare the *Lycorhinus* holotype (Fig. 8) directly with the dentary and lower teeth of *Heterodontosaurus* (Fig. 10). Thulborn, drawing his *Lycorhinus* characters from the holotype and not from A.100, can claim only three points of similarity: the presence of a prominent caniniform first dentary tooth, the planing-off of the lateral sides of the mandibular crowns to produce sharp chisel-like ends, and the size gradation of those mandibular crowns so that the largest are in the middle of the tooth row. (It is not clear from his paper (p. 243) whether the size gradation is supposed to pertain to the upper cheek teeth only or to the lower teeth as well, but it does in fact pertain to both.) We indeed agree that all three features appear to be present in both genera. On the other hand, Thulborn admits to one difference: the lower caniniform is crenellated only on its anterior edge in *Lycorhinus*, on both edges in *Heterodontosaurus*. There are also other important differences, unrecognized by Thulborn. Haughton (1924) mentioned that the 'molars' of *Lycorhinus* had a pronounced cingulum, which, as pointed out by Crompton & Charig (1962), is absent in the postcaniniforms of *Heterodontosaurus*. The crowns of *Lycorhinus* taper down towards that cingulum so that, although they touch their neighbours occlusally, large triangular gaps are left between their more basal portions; the latex impression shows that their lateral surfaces are convex in both directions, vertical and horizontal. In *Heterodontosaurus*, by contrast, the lateral surface of each lower postcaniniform crown has sub-parallel edges which touch (or almost touch) its neighbours throughout its length and is more or less flat. There is a further difference in the vertical ridging-and-grooving on the medial surface of the teeth: in *Lycorhinus* a narrow groove lies behind a wide anterior ridge, in *Heterodontosaurus* a wide shallow trough lies behind a narrow anterior ridge. Because the similarities between *Lycorhinus* and *Heterodontosaurus* are so few and so general (indeed, they could well be family characters rather than generic) we regard the generic identity of *Lycorhinus* and *Heterodontosaurus* as unproven; because there are also certain differences between them, we consider it unlikely. As we wrote in 1962: 'This [the possession by *Lycorhinus* of a distinct cingulum] and the nature of the wear of the teeth appear to indicate that *Heterodontosaurus* and *Lycorhinus* are generically distinct.' We see no reason to change our minds; rather has our detailed analysis confirmed our opinion. The fragmentary nature and poor preservation of the *Lycorhinus angustidens* holotype, taken together with the fact that it is now represented only by an impression, make it improbable that the matter could ever be settled really conclusively one way or the other, and for that reason we prefer to regard the names *Lycorhinus* and *L. angustidens* as *nomina dubia*, names which have been founded on inadequate material and which ought not to be used except in connection with the holotype itself.

Adoption of this point of view is not only *sufficient* in itself to justify rejection of any synonymy involving the name *Lycorhinus* but logically *requires* such rejection. Charig (in press) states that '. . . no worker can be compelled to accept

the validity of a specific or generic name based on type-material which he considers unsatisfactory; if he rejects such a name it becomes—to him—a *nomen dubium*, and on those grounds he is not only entitled to reject other authors' synonymies involving the name in question but is logically *obliged* to do so'.

The alleged identity of the lower jaw of A.100 (Fig. 4) with that of *Heterodontosaurus tucki* (Fig. 10) is another matter. Comparison of the postcaniniform teeth is difficult because specimen A.100 includes only anterior dentary teeth (numbers 1–7) and the *H. tucki* holotype includes only the caniniform and the more posterior teeth (numbers 1 and probably 7–14); further, the lower jaw of A.100 and its teeth are exposed only on the lateral side, while the lower teeth of *H. tucki*, though visible in both aspects, are *well* exposed only on the medial side. Even so, the alleged identity is easy to disprove, for though the similarities are few the differences are many. In fact, a list of those differences is essentially the list of differences between A.100 and the *Lycorhinus angustidens* holotype given earlier in this article together with another couple of differences between *Lycorhinus* and *Heterodontosaurus* as given immediately above. We shall put these down in tabular form. Let us include also a column for the corresponding condition in the *Lycorhinus* holotype—where known—and insert it between the A.100 and *Heterodontosaurus* columns (the reason for this arrangement will soon become apparent). Let us include also two additional characters in which A.100 differs from *Lycorhinus* but which are not visible in the holotype of *Heterodontosaurus tucki*.

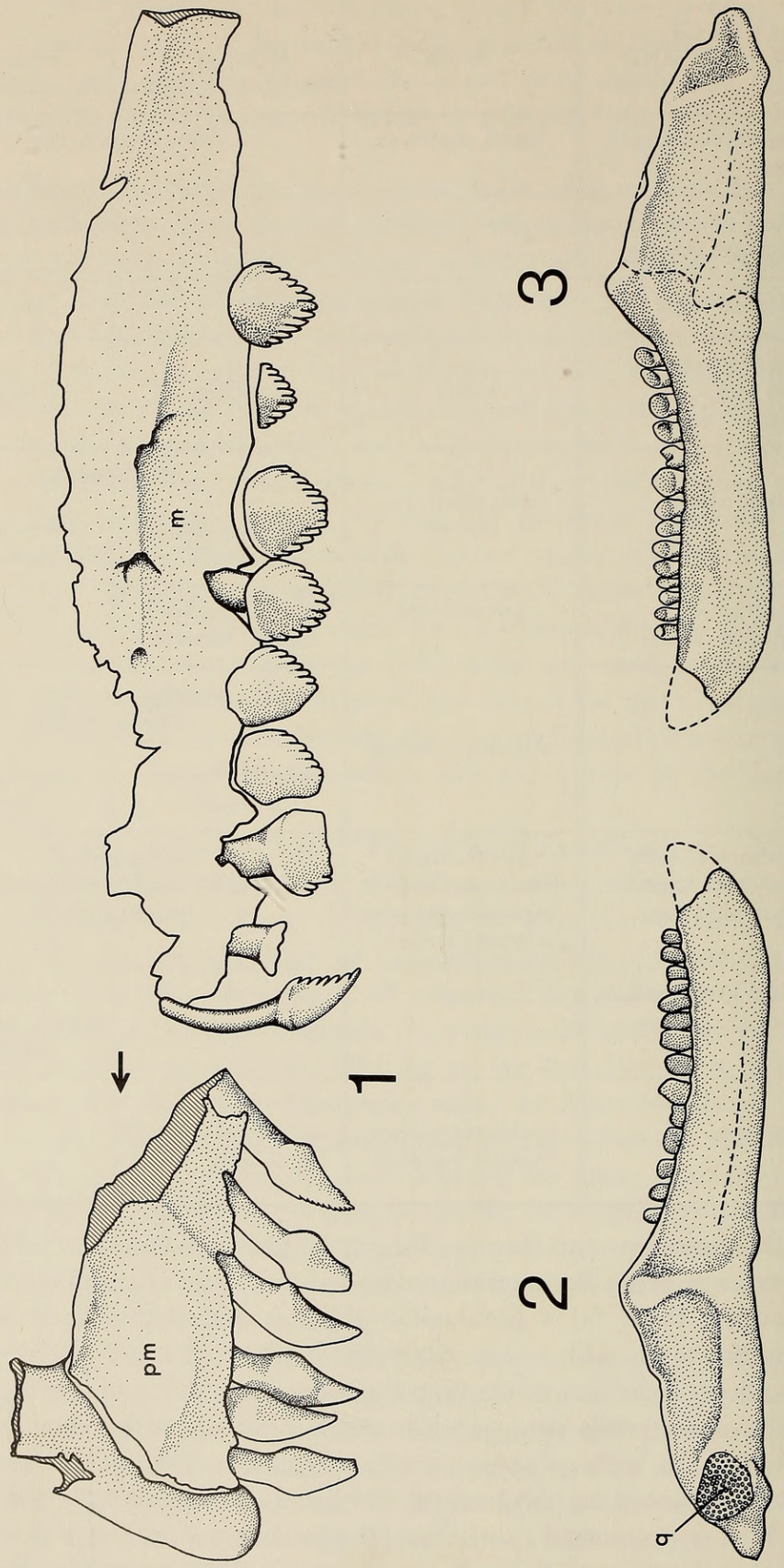
Thulborn also writes (p. 243): 'The teeth of *Lycorhinus* [viz., A.100] bear on their labial surfaces median ribs which are neither as thin nor as sharp as those in *Heterodontosaurus*.' From the context he could be referring to vertical ridges on either the lateral surface or the medial surface of either the upper or the lower teeth of *Heterodontosaurus*, all of which are different. On the next page (p. 244), where he is presumably referring to the same feature, he partly clarifies the situation by writing: 'Fluting on the labial surfaces of the cheek teeth is more pronounced in the species *tucki*.' In *Heterodontosaurus*, however, there are no thin sharp median ridges on the lateral surfaces of the *lower* teeth, indeed all that is known of the ornamentation of the lower teeth in the type of *H. tucki* (where they were badly damaged during development) is that a broad vertical ridge appears to have been present; yet a comparison of the lateral surface of the lower teeth of A.100 with the lateral surface of the *upper* teeth of *Heterodontosaurus* would mean nothing.

It is obvious from the comparative table that A.100 is the least specialized and *Heterodontosaurus* the most specialized of the three forms, with *Lycorhinus angustidens* fitting in as an intermediate. This accords with their stratigraphical positions: A.100 and *Lycorhinus* are from the same locality and therefore from approximately the same horizon within the Red Beds, *Heterodontosaurus* is from the overlying Cave Sandstone and is likely to be a little younger.

Heterodontosaurus tucki (Figs 10, 11) and A.100 (Figs 5–7) may also be com-

COMPARISON OF LOWER JAWS AND TEETH		A.100	Holotype of *Lycorhinus angustidens*	Holotype of *Heterodontosaurus tucki*
depth of mandible beneath caniniform		much shallower	exceptionally deep	
caniniform tooth	width of base at alveolar margin	more slender	broader	
	crenellate edges	anterior edge only		both edges
width of gap between caniniform and second dentary tooth		wider	narrower	? (not seen)
postcaniniform teeth	distance apart	well apart, no contact	close together: crowns in contact distally	close together: crowns in contact throughout length
	inclination of anterior teeth	not inclined	crowns inclined slightly forwards	? (not seen)
	wear	virtually unworn	heavily abraded to form continuous occlusal surface: occlusal surface irregular	heavily abraded to form continuous occlusal surface: occlusal surface smooth
	appearance of each crown in lateral or medial view	symmetrical (shown by cusps & ridging-&-grooving on lateral surface)	asymmetrical (shown by ridging-and-grooving on medial surface)	
	distinct neck between root and crown	present	?	absent, teeth essentially columnar
	cingulum	present: on lateral surface (medial not seen)	present: on medial surface only	absent

pared on the upper jaw and the rest of the skull, parts which are lacking entirely in *Lycorhinus angustidens*. Both specimens have (*a*) a large, triangular and widely open antorbital fossa, (*b*) a premaxilla which is remarkably deep below the external naris, (*c*) a wide, deep diastema between the premaxilla and the maxilla, and (*d*) a distinct recess, forming a 'step', in the lateral surface of the maxilla above the tooth row (possibly more pronounced in *Heterodontosaurus* than in A.100). In both specimens a wide edentulous zone at the front of the premaxilla is followed by three teeth, the first two being simple conical pegs and the third a prominent caniniform (large, but not as large as the lower caniniform) with its posterior border crenellate (in *Heterodontosaurus* the anterior


m
pm
1
2
3
q

border is not visible). The maxillary teeth number about a dozen (12 in *Heterodontosaurus*, 13 in A.100) with the largest crowns in the middle of the series; their medial sides are planed off to produce sharp, chisel-like ends. This planing-off is oblique in *Heterodontosaurus*; in A.100, however, although Thulborn does mention in his text (p. 243) that the medial sides of the maxillary teeth are planed off, his Figure 4 gives no indication whatever of this character.

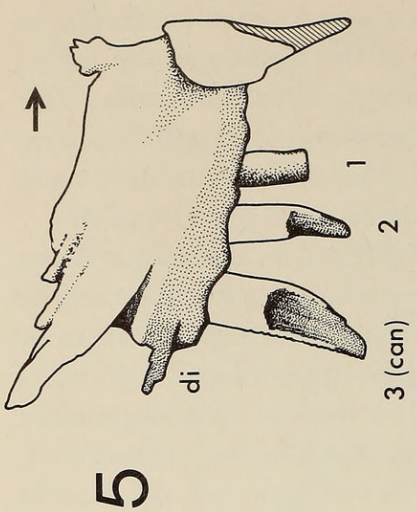
On the other hand, there are also a number of differences. Specimen A.100 seems to lack the suborbital boss and the jugal process which are so characteristic of the jugal of *Heterodontosaurus*, indeed the whole form of the jugal seems to be very different. The disparity between the lengths of the upper caniniform and of the other premaxillary teeth is less marked in A.100 than in *Heterodontosaurus*. In *Heterodontosaurus* the most anterior tooth in the maxilla lies immediately beneath the anterior end of the antorbital fossa; in A.100, however, the maxilla itself and its tooth row extended forwards far beyond the limits of that fossa. The maxillary teeth of *Heterodontosaurus* are close together, with only small gaps between them at the alveolar margin and touching each other occlusally, even overlapping a little in most instances; but those of A.100 are separated by wide gaps at the alveolar margin, sometimes wider than the teeth themselves. The maxillary teeth of *Heterodontosaurus* possess no neck and are essentially columnar in form, while those of A.100 have a pronounced neck and cingulum demarcating the root from the crown. In *Heterodontosaurus* the lateral surface of each maxillary tooth bears three prominent ridges—anterior, central and posterior—separated by sharply defined excavated regions, the central ridge in particular being thin and sharp; the medial surface, however, is quite different in that it has only a poorly developed central ridge. In A.100, by contrast, the lateral and medial surfaces of the maxillary teeth are essentially alike, the central ridges being weaker, thicker and blunter than on the lateral surfaces of the maxillary teeth of *Heterodontosaurus*.

Fig. 1. Fabrosaurid gen. et sp. indet. Described and figured Thulborn 1970*b*, 1971*a* as *Fabrosaurus australis*. Department of Zoology, University College London, field no. B.17. Likhoele Mountain, near Mafeteng, Lesotho; Red Beds. Left premaxilla and maxilla. Lateral view, × $3\frac{3}{4}$. (After Thulborn 1971*a*; maxilla reversed from right side.)

Fig. 2. *Pisanosaurus mertii* Casamiquela, 1967. Holotype. Laboratorio de Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina, no. 2577. 'Agua de las Catas', opposite Km 461 on Ruta Nacional no. 40, La Rioja Province, Argentina; middle section of Ischigualasto Formation. Left mandible. Medial view, × $\frac{3}{4}$. (After Bonaparte, in press; reversed from right side.)

Fig. 3. Same individual. Left mandible. Lateral view, × $\frac{3}{4}$. (After Bonaparte, in press; reversed from right side.)

Abbreviations: m—maxilla; pm—premaxilla; q—fragment of the quadrate.



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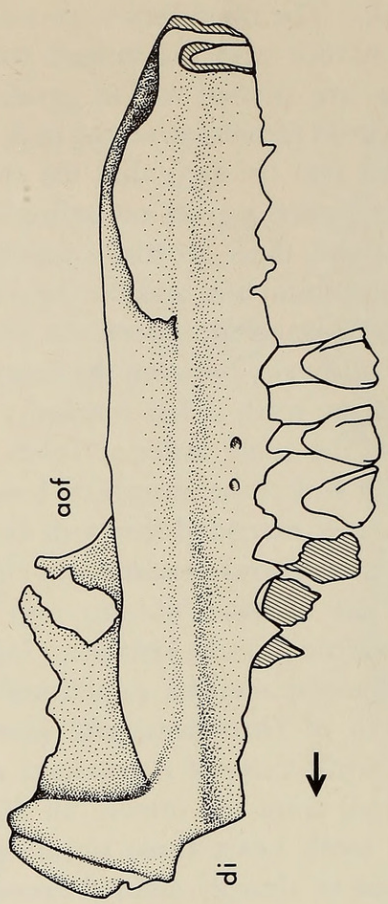

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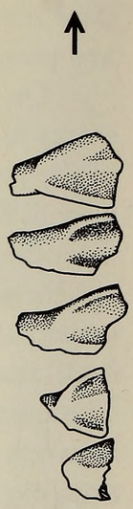

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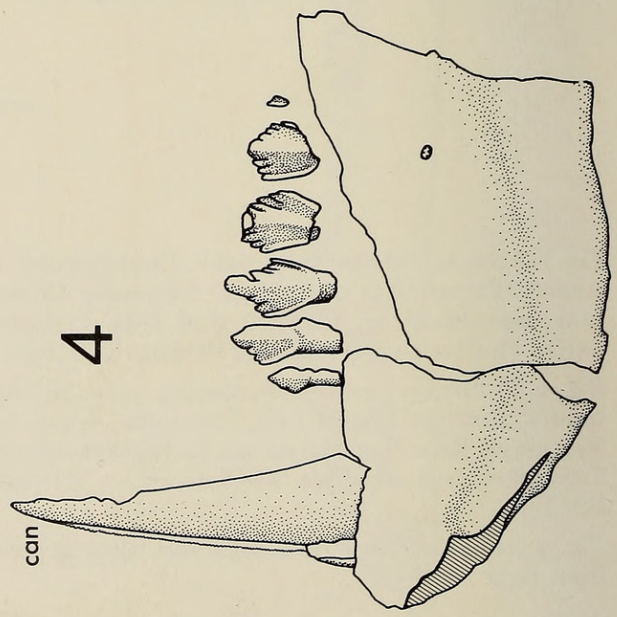

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All the premaxillary teeth of *Heterodontosaurus* (including the caniniform) appear to have more or less rounded tips; but they are seen only in lateral view, and it is not possible to be sure that they do not have wear facets on the medial side like those of A.100 which, Thulborn suggests, 'resulted from their working against a horn-sheathed predentary at the mandibular symphysis'.

There are also certain very characteristic features of the cheek teeth of *Heterodontosaurus*, both upper and lower, which cannot be used in this comparison because Thulborn does not mention the corresponding condition in the latter specimen. In *Heterodontosaurus* the cheek teeth are curved in the transverse plane so that, in anterior or posterior view, the lateral profile of each upper crown is convex with a distinct 'knee', the medial profile is more or less straight, and the planar occlusal surface faces medioventrally; the opposite holds true for the lower crowns, though their convexity (on the medial side) is weaker. There is an extremely thin layer of enamel on the occlusal half of each convex surface only, i.e. on the lateral surface of each upper tooth and the medial surface of each lower tooth. Thulborn does state, however, that the *unworn* cheek teeth of *Lycorhinus* (by which he presumably means the lower postcaniniform teeth of A.100) are completely enamelled.

In this connection it may be noted that Galton (1973) reproduces (fig. 2 K) Thulborn's figure 3 of the right maxilla of A.100; his new caption reads: '*Heterodontosaurus* sp., right maxilla in lateral view, figured as *Lycorhinus augustidens* by Thulborn (1970*a*) who does not and cannot demonstrate that this specimen is identical to the lost holotype of *Lycorhinus angustidens* Haughton (1924).' While we agree with Galton that A.100 cannot be referred to *Lycorhinus angustidens*, we would certainly not place it in the genus *Heterodontosaurus* (see our conclusions below); the differences between A.100 and the type of *H. tucki* are too many and too substantial.

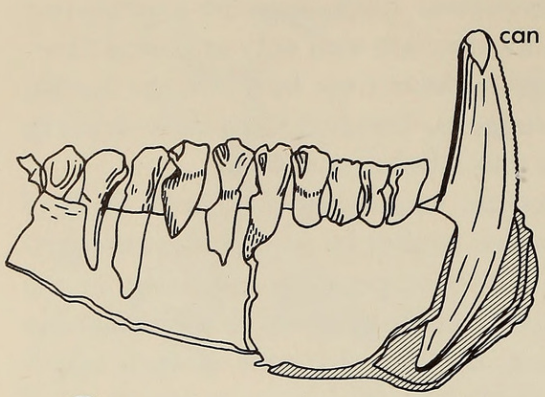
Fig. 4. Heterodontosaurid gen. et sp. indet., described and figured Thulborn 1970*a* as *Lycorhinus angustidens*. Department of Zoology, University College London, no. A.100. Paballong, near Mount Fletcher, Herschel District, Cape Province, South Africa; Red Beds. Left dentary, with teeth. Lateral view, × 2. (After Thulborn 1970*a*; reversed from right side.)

Fig. 5. Same specimen. Left premaxilla, with teeth. Medial view, × 2. (After Thulborn 1970*a*; reversed from right side.)

Fig. 6. Same specimen. Left maxilla, with teeth. Lateral view, × 2. (After Thulborn 1970*a*; reversed from right side.)

Fig. 7. Same specimen. Left maxillary teeth. Medial view, × 2. (After Thulborn 1970*a*.)

Abbreviations: aof—antorbital fenestra; can—caniniform tooth; di—diastema.



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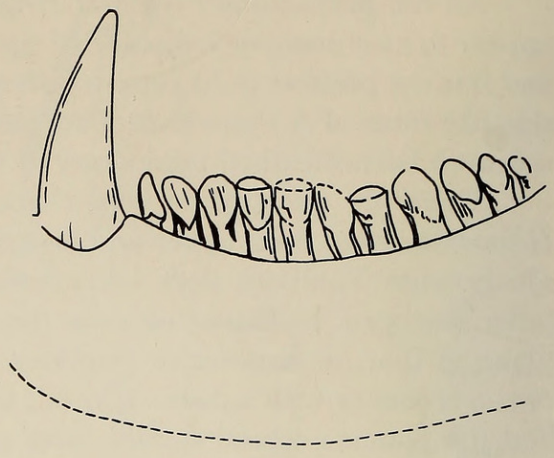

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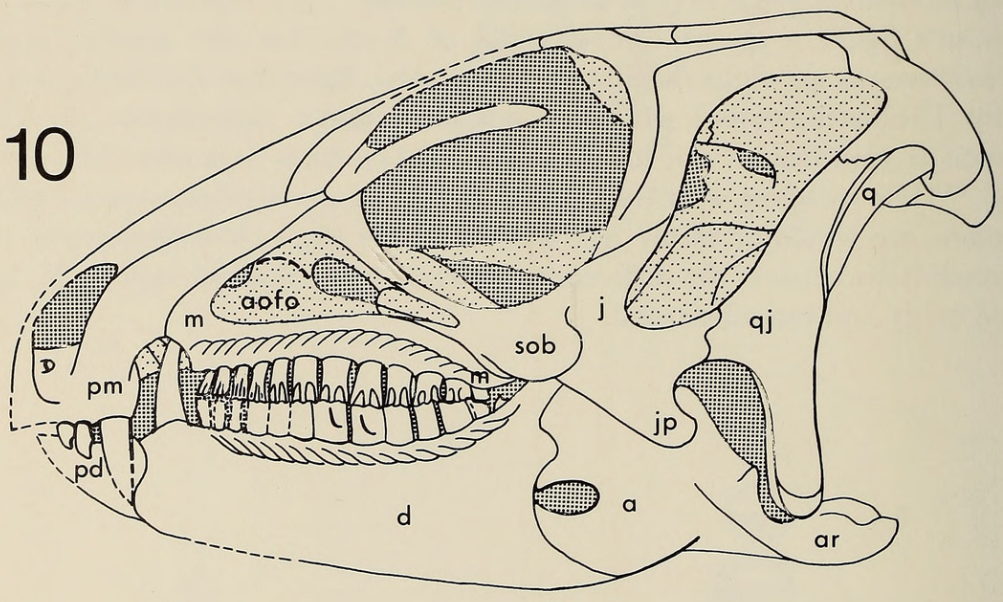

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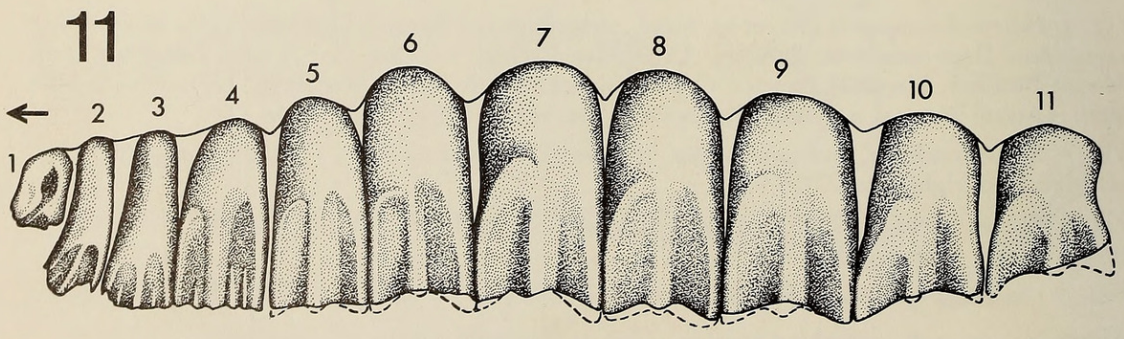

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If it be accepted that the whole of specimen A.100 represents a single individual, then certain characters of the upper jaw and its teeth also accord with the view that A.100 is less specialized than *Heterodontosaurus*. They include the simpler form of the jugal (without suborbital boss or jugal process), the slightly weaker development of the upper caniniform, the wider spacing of the maxillary teeth in the tooth row, the simpler form of those teeth with lateral and medial surfaces more or less alike, and possibly a lesser development of the recess and 'step' in the lateral surface of the maxilla above the tooth row.

The graded differences between A.100, *Lycorhinus* and *Heterodontosaurus* are indeed significant; but, as mentioned above, they do not obscure the essential similarities of the three forms—some of them unique to the group. There are three characters which are diagnostic of the group, no matter what rank the latter may be accorded in the classification: the prominent caniniform at the front of the dentary, a trend towards the possession of closely packed postcaniniform teeth with antero-posteriorly expanded crowns worn down to a continuous occlusal surface (not evident in the lower jaw of A.100), and the concavity extending along the outer sides of the maxilla and dentary above and beneath the postcaniniform tooth row (suggesting a mediad recession of the tooth row into the side of the face). We believe that this suite of common characters justifies the association of the forms in question into a taxon of suprageneric rank—the family Heterodontosauridae.

The three specimens considered here also share a unique peculiarity in that their teeth show no signs of replacement. It seems, however, that this character is not invariably associated with the rest of the suite; we have the incomplete maxilla of what appears to be another heterodontosaurid from

Fig. 8. *Lycorhinus angustidens* Haughton, 1924. Holotype. South African Museum, no. 3606. Paballong, near Mount Fletcher, Herschel District, Cape Province, South Africa; Red Beds. Left dentary, with teeth. Medial view, × 1⅕. (After Haughton 1924.)

Fig. 9. Same individual, same bone. Lateral view, × 1⅕. (After Broom 1932.)

Fig. 10. *Heterodontosaurus tucki* Crompton & Charig, 1962. Holotype. South African Museum, no. K337. Mountain behind Tyindini trading store, Herschel District, Cape Province, South Africa; Cave Sandstone. Reconstruction of skull. Left lateral view, natural size. (After Charig & Crompton, in press; reversed from right side.)

Fig. 11. Same individual. Left maxillary teeth. Lateral view, × 4. (After Charig & Crompton, in press; reversed from right side.)

Abbreviations: a—angular; aofo—antorbital fossa; ar—articular; can—caniniform tooth; d—dentary; j—jugal; jp—jugal process; m—maxilla; pd—predentary; pm—premaxilla; q—quadrate; qj—quadratojugal; sob—suborbital boss. On all the illustrations the arrow indicates the anterior direction.

the Stormberg Series with functional teeth possessing the typical characters of the family but also with two unerupted replacing teeth and other evidence of replacement. This is the fragment referred to by Thulborn (1970*a*: 243) as 'A second specimen of *Heterodontosaurus*'.

The relative sizes of specimen A.100, *Lycorhinus* and *Heterodontosaurus* may be of interest. Comparisons are difficult, but the average interval at which the teeth are inserted in the middle of the dentary seems to be about the same (3,6 mm) in all three. The depth of the dentary beneath those teeth, however, is a little greater in specimen A.100 than in either *Heterodontosaurus* or *Lycorhinus*, and the maxilla is approximately one-third longer in A.100 than in *Heterodontosaurus*.

Also relevant to our discussion is the genus *Pisanosaurus* Casamiquela, 1967 (only species *P. mertii* Casamiquela, 1967 from the Ischigualasto Formation of Argentina), which is of Carnian or perhaps even of Ladinian age; it is therefore older than the African forms with which this paper is mainly concerned and which are generally considered to be Norian or Rhaetian. Indeed, *Pisanosaurus* is the earliest ornithischian known. The unique holotype comprises a fragment of maxilla and an almost complete mandible (Figs 2, 3), both with teeth; cervical, dorsal and (as natural moulds) sacral vertebrae; a little rib material; an incomplete scapula and an impression of part of the pelvis; the impressions of three metacarpals; and a good part of the hind limb. *Pisanosaurus* has been variously placed in the families Pisanosauridae (Casamiquela 1967), Hypsilophodontidae (Thulborn 1971*b*[2], 1972; Galton 1972, 1973) and Heterodontosauridae (Bonaparte, in press). The last work cited, a redescription and reassessment of *Pisanosaurus*, shows that it possesses all the heterodontosaurid tooth characters mentioned above and several others too, with the notable exception of the caniniform teeth; and even the absence of those teeth is by no means certain because *Pisanosaurus* lacks both the premaxilla and the front end of the mandible—a sufficient length thereof to have borne a caniniform. Galton (1972, fig. 1) indicates his belief that *Pisanosaurus* occupies a position in ornithischian phylogeny at the base of the ornithopod line of ancestry, just after the diverging of the heterodontosaurid, ankylosaur and stegosaur lines; indeed, he places it on or close to the line of ancestry of all other ornithischians except *Fabrosaurus* and *Echinodon*. He therefore regards it as the earliest and most primitive hypsilophodontid, for he writes (p. 466): 'All hypsilophodonts were probably derived from a form similar to *Pisanosaurus*.'

It seems to us, however, that Bonaparte's revelation of the specialized, truly heterodontosaurid character of the *Pisanosaurus* dentition makes Galton's beliefs completely untenable; we therefore support Bonaparte's reference of the genus to the Heterodontosauridae, a family known otherwise only from southern Africa. But the higher tooth count (maxillary teeth estimated at 16–18 by Bonaparte, 15 dentary teeth actually preserved) suggests that *Pisanosaurus* is

[2] Thulborn (1971*b*) includes *Pisanosaurus* among the 'fabrosaur group' of the family Hypsilophodontidae. The separate family Fabrosauridae was formally proposed by Galton in 1972.

more primitive than its African relatives; this suggestion, which will probably be confirmed by other characters of the genus when they become known, accords with its lower stratigraphical position.

Our conclusions may be summarized as follows:

1. All three specimens considered here—holotype of *Lycorhinus angustidens*, holotype of *Heterodontosaurus tucki* and specimen A.100—are sufficiently alike to be placed in the same family, for which the correct name is Heterodontosauridae. The diagnostic characters of that family are the prominent caniniform tooth at the front of the dentary (and in the premaxilla too where known), a trend towards the possession of closely packed postcaniniform teeth which are worn down to a continuous occlusal surface, and the mediad recession of the postcaniniform tooth row into the outer side of the jaws. The three specimens concerned are also remarkable in their apparent total lack of tooth replacement, but this cannot be regarded as an absolutely diagnostic character because another heterodontosaurid jaw fragment from the Stormbergs shows unequivocal evidence of replacement.
2. Whether the lower jaw of A.100 did in fact belong to the same individual as the other skull elements, or even to the same species, might be considered a little doubtful because of the unworn nature of the lower teeth and the heavily worn nature of the uppers. On the other hand, the various skull elements of A.100 show no duplication, they are all of commensurate size, and both upper and lower jaws give clear indications of heterodontosaurid affinities.
3. The lower jaw of A.100, however, is sufficiently distinct from *Lycorhinus* and *Heterodontosaurus*, and the upper jaw (unknown in the former genus) is sufficiently distinct from *Heterodontosaurus*, to rule out any possibility that A.100 might be congeneric with either. It must represent a new genus of heterodontosaurid from the Upper Trias of southern Africa.
4. *Lycorhinus angustidens*, as far as can be seen in so imperfect a specimen, bears a strong resemblance to *Heterodontosaurus tucki* but differs sufficiently in certain details of tooth structure to rule out any possibility of conspecificity. The fragmentary nature, poor preservation and subsequent loss of most of the *Lycorhinus angustidens* holotype make it impossible to determine whether or not the two forms were congeneric, but without positive evidence of congenericity we are obliged to regard them as separate genera. In any case, we consider the names *Lycorhinus* and *L. angustidens* to be *nomina dubia*.
5. If all three lower jaws be compared together, *Heterodontosaurus* and A.100 seem to be very different; *Lycorhinus* is intermediate between them, resembling *Heterodontosaurus* rather than A.100 in most of the contrasting characters but more like A.100 in a few. A.100 is the most primitive of the three and *Heterodontosaurus* the most specialized. This is borne out by a comparison of the upper jaws and teeth (also the jugal) of A.100 with the corresponding elements of *Heterodontosaurus*.

6. The slightly earlier genus from Argentina, *Pisanosaurus*, is also a heterodontosaurid, probably more primitive than the forms from southern Africa but certainly too specialized to be ancestral to any post-Triassic ornithischians known.
7. As will be shown elsewhere, the heterodontosaurids possessed highly specialized masticatory and locomotor adaptations which indicated that they had moved into ecological niches quite distinct from those occupied by other contemporary dinosaurs, both ornithischian and saurischian. Diversity at the generic level might therefore be expected.

Acknowledgments

We are grateful to Dr T. H. Barry, Director of the South African Museum, Cape Town, for allowing us access to the holotype of *Heterodontosaurus tucki*; likewise to Dr J. F. Bonaparte, of the Fundacion Lillo of the Universidad Nacional de Tucumán, Argentina, for permitting us to refer to his unpublished manuscript on *Pisanosaurus* and to reproduce two text-figures therefrom.

References

Bakker, R. T. & Galton, P. M. 1974. Dinosaur monophyly and a new class of vertebrates. *Nature, Lond.* **248**: 168–172.

Bonaparte, J. F. In press. *Pisanosaurus mertii* Casamiquela and the origin of the Ornithischia. *J. Paleont.*

Broom, R. 1911. On the dinosaurs of the Stormberg, South Africa. *Ann. S. Afr. Mus.* **7**: 291–308.

Broom, R. 1932. *The mammal-like reptiles of South Africa and the origin of mammals.* London: Witherby.

Casamiquela, R. M. 1967. Un nuevo dinosaurio ornitisquio triásico (*Pisanosaurus mertii;* Ornithopoda) de la Formación Ischigualasto, Argentina. *Ameghiniana* **5**: 47–64.

Charig, A. J. In press. Thoughts on synonymy. *Palaeontology.*

Charig, A. J. & Crompton, A. W. In press. The Triassic ornithischian *Heterodontosaurus tucki:* skull, dentition and systematic relationships. *Ann. S. Afr. Mus.*

Charig, A. J. & Reig, O. A. 1970. The classification of the Proterosuchia. *Biol. J. Linn. Soc.* **2**: 125–171.

Crompton, A. W. & Charig, A. J. 1962. A new ornithischian from the Upper Triassic of South Africa. *Nature, Lond.* **196**: 1074–1077.

Edmund, A. G. 1969. Dentition. *In:* gans, c., bellairs, a. d'a. & parsons, t. s., *eds. Biology of the Reptilia.* **1**: 117–200. London, New York: Academic Press.

Galton, P. M. 1972. Classification and evolution of ornithopod dinosaurs. *Nature, Lond.* **239**: 464–466.

Galton, P. M. 1973. The cheeks of ornithischian dinosaurs. *Lethaia* **6**: 67–89.

Ginsburg, L. 1964. Découverte d'un scélidosaurien (dinosaure ornithischien) dans le Trias supérieur du Basutoland. *C. r. hebd. Séanc. Acad. Sci., Paris* **258**: 2366–2368.

Haughton, S. H. 1924. The fauna and stratigraphy of the Stormberg Series. *Ann. S. Afr. Mus.* **12**: 323–497.

Kermack, K. A., Mussett, F. & Rigney, H. W. 1973. The lower jaw of *Morganucodon. Zool. J. Linn. Soc.* **53**: 87–175.

Kuhn, O. 1966. *Die Reptilien, System und Stammesgeschichte.* Krailling bei München: Oeben.

Owen, R. 1861. On the fossil Reptilia of the Wealden and Purbeck Formations: Part 5 (Lacertilia). *Palaeontogr. Soc.* [*Monogr.*]: 31–39.

ROMER, A. S. 1956. *Osteology of the reptiles*. Chicago: University of Chicago Press.
ROMER, A. S. 1966. *Vertebrate paleontology*. 3rd ed. Chicago, London: University of Chicago Press.
THULBORN, R. A. 1970*a*. The systematic position of the Triassic ornithischian dinosaur *Lycorhinus angustidens*. *Zool. J. Linn. Soc.* **49**: 235–245.
THULBORN, R. A. 1970*b*. The skull of *Fabrosaurus australis*, a Triassic ornithischian dinosaur. *Palaeontology* **13**: 414–432.
THULBORN, R. A. 1971*a*. Tooth wear and jaw action in the Triassic ornithischian dinosaur *Fabrosaurus*. *J. Zool., Lond.* **164**: 165–179.
THULBORN, R. A. 1971*b*. Origins and evolution of ornithischian dinosaurs. *Nature, Lond.* **234**: 75–78.
THULBORN, R. A. 1972. The post-cranial skeleton of the Triassic ornithischian dinosaur *Fabrosaurus australis*. *Palaeontology* **15**: 29–60.